Observations on the germination of Phoradendron villosum and P. californicum

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A few years since, when in California, I had the opportunity of studying the structure and noting certain physiological peculiarities of *Phoradendron villosum.** The study was confined almost entirely to mature forms, only a few relatively young plants were secured, and no seedlings were seen although I searched diligently for them. Neither was I successful in germinating the seeds. It is with the idea of supplementing that work with some account of the younger stages of the life history of the mistletoe that this sketch is presented.

Among other things I showed in the preceding paper that the spreading of the mistletoe in the host occurs in the cortex only, a fact well known, and also that this takes place because the haustoria are supplied with secreting cells from which probably exudes a solvent capable of dissolving the cell-walls of the host. It however was noticed that not all of the host-tissues were affected by the haustoria. For instance, their enzymes were apparently incapable of dissolving the suberized walls of the cork as well as the lignified grit-cells in the cortex, and this may account in part for the fact that the haustoria do not penetrate into the woody central portion of the stem. Of course in the latter instance other questions enter, as for instance the necessary change in function of the haustoria to water-absorbing organs, but as regards the grit-cells there can be no doubt. These were frequently noted lying within the tissues of the parasite and completely enclosed by them, which means that at an early stage in the development of the plant the grit-cells, like the other and adjacent cortical cells of the host, came into contact with the solvent secreted by the

* The anatomy of *Phoradendron villosum* Nutt. Bull. Torrey Club, 28: 374. 1901.

Kerner and Oliver. Natural history of plants. 1: 216. — Peirce. On the structure of the haustoria of some phanerogamic parasites. Ann. Bot. 7: 317. 1893.

parasite, but they, with lignified walls, unlike the latter whose walls were unmodified, were unaffected by this fluid.

The question at once arises as to whether the seedlings of the mistletoe secrete enzymes which can dissolve suberized, cuticularized or lignified cell-walls, and thereby gain entrance into the host at nearly any point, or, as may be the case in the haustoria of mature plants, only unmodified walls are affected. Of course it may be that cuticularized walls can be dissolved and neither of the other two. I have no evidence to offer in the latter alternative, but it is noticeable that the mistletoe is almost never parasitic on itself* in spite of the fact, which will be given later, that the seedlings often germinate in contact with its own branches. Dr. MacDougal informs me, however, that several instances have been known of the parasitism of one loranth on another in Jamaica. The mistletoe is provided with a cuticularized epidermis with communication to the exterior through stomates only.

In the vicinity of the Desert Botanical Laboratory occur two species of mistletoe, *P. villosum* and *P. californicum*. The former has white berries and broad leaves, the latter has red berries and is nearly devoid of leaves. *P. villosum* occurs here mainly on the native ash and native cottonwood and appears to be quite like the California plant studied by me. The other species has a different habit of growth. It generally hangs from the branches of the host, and is found mainly on the cat-claw (*Acacia Greggii*), and mesquite (*Prosopis juliflora*). I have seen it also on palo verde (*Parkinsonia microphylla*); and I believe that it occurs on the creosote bush (*Covillea tridentata*), but I have not seen it on this plant.

The distribution of the mistletoe from tree to tree is likely always effected by the agency of birds, but its distribution in a tree may be brought about in another manner also, and thus it is frequently accounted for by the position of the older plants. In cases where infection has occurred on the higher branches of the host it frequently happens that numerous younger plants of the parasite will be placed directly under this pioneer, as if they

* In Kerner and Oliver's work, *l. c.*, it is said that on one occasion mistletoe, probably *Viscum*, was seen growing on *Loranthus*. It, however, is not clear whether the place where the *Viscum* seedling gained an entrance was cuticularized or suberized.

were derived from its seeds. This habit is of much use to the collector, since he has but to mark a tree in which a large bunch of mistletoe is growing in the top, and if there is sufficient growth beneath, he is sure to find at the proper time of the year an abundance of seedlings.

Thus it must frequently happen that the mistletoe seeds germinate without having been first passed through the alimentary tract of birds, and, in fact, although I did not determine more closely the conditions under which they best germinate, these do not appear to be other than that the seeds must be mature. A large amount of heat is not required, and also it may be that germination is not dependent on rains.

In February, March and April germinating seeds of both species of mistletoe were seen in great abundance. The seedlings were found on all portions of the mesquite, including leaves, and on cat-claw and ash. That is, the seeds germinated on the old bark at the base of the tree as well as on last year's growth. I observed them also on dead twigs that were detached from any tree, on mesquite thorns, and even on the mistletoe itself. Also seedlings of *P. californicum* were taken from branches of the ash whither the seeds had been carried by birds. It thus appears questionable whether the character of the substratum has any influence whatever on the germination of the mistletoe seeds.

It is of interest to note that the seeds of the mistletoe are for the most part ripe and fallen by the time the leaves of the host make their appearance. This has one great advantage to the parasite, namely, that of being better able to reach the twigs and branches of the host than would be the case when these members are covered with leaves. As it will be seen later this is especially important in the case of the mesquite and its mistletoe.

Although water may not be a factor in inducing the germination of the seeds, it may assist in their dissemination; however I have made no direct observation on this point. When the seeds fall and become attached to a branch, they are so firmly fastened by means of the adhesion to the branch of their viscid contents, that they are dislodged with difficulty (FIGURE 1). It is quite possible, and here again I have no proof of the truth of the statement, that the firmness of the attachment is of considerable importance

to the seedling in permitting it to press the tip of the radicle firmly against the host.

After attachment is secured, the radicle is sent out; it turns in most cases directly toward the host and comes into contact with

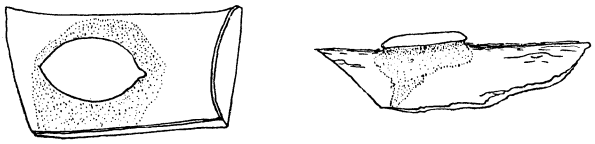

FIGURE 1. Seeds of *P. villosum*, showing manner of attachment to the cottonwood branch. The shaded area represents the viscid substance which glues the seeds to the host.

it, and not until then forms the expanded tip whose distal epithelium functions as the secreting organ. The color, form and size of the hypocotyl in the two species of mistletoe are unlike. The hypocotyl of *P. californicum* is slender, reddish in color and may

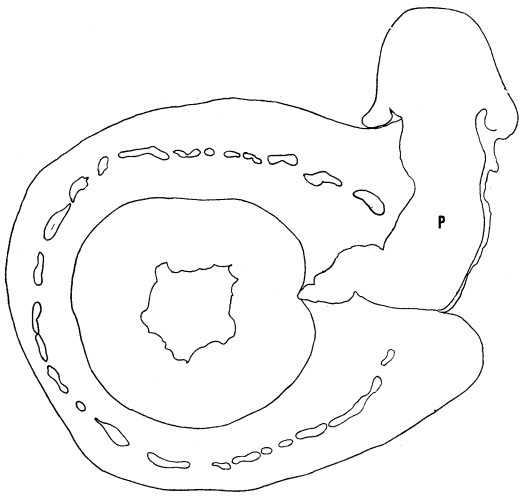

FIGURE 2. Seedling of *P. villosum* on cottonwood. This seedling penetrated last season; the tip of the haustorium is being transformed into a sinker for the absorption of water.

attain a length of .7 cm. although it is usually shorter. The hypocotyl of the other form is short, rarely much exceeding the seed-coat, stout and greenish in color. The structure of the hypocotyl in both is clearly like that of the mature plants, *i. e.*, the outer epi-

dermal wall is strongly cuticularized, and hence the hypocotyl is xerophytic. This not only ensures against rapid drying out but probably the converse of that, making impossible, perhaps, the absorption of water should it chance to come during the early stages of germination.

The cotyledons probably never emerge from the seed until foothold has been secured by the root, and this may not take place under several months from the time germination commences; they are thus unlike those of *Loranthus*, which appear much more quickly.* FIGURE 2 shows a young plant of *P. villosum* on a cottonwood branch. It was collected in January and the seed presumably was one that ripened and began to germinate the previous season. The seed-leaves, however, had not yet left the seed-coat; they were closely pressed together like the young leaves in old plants.

There are three well-marked periods in the life of the young mistletoe plant: 1, the growth of the hypocotyl and the formation of the disc; 2, penetration; and 3 (probably after the establishment of a connection with a water supply), the erection of the cotyledons.

Some very interesting work is to be done on the causes that influence the radicle to turn towards the host. In *P. villosum* this almost always occurs at once but in the other species the radicle may bend and twist in a variety of ways before the host is touched. However, in the end the tip of the radicle touches the substratum and flattens into a disc-shaped organ, likely as a result of the pressure caused by the resistance of the host.† The young disc was not especially studied; it has been long known that it secretes a substance which aids the penetration of the haustorium. The discs increase in size by the multiplication of cells about the periphery, and in older forms, in which penetration has already taken place, secreting cells of the disc are confined to the outer portion (FIGURE 3). These are as usual elongated, they have dense protoplasmic content and conspicuous nuclei.

Penetration is effected unlike in the two species, and in the instances cited, the manner of penetration is dependent on the

* Keeble. Loranthaceae of Ceylon. Trans. Linn. Soc. London, II. 5: 91. 1895.

† Compare the account given in Engler & Prantl, Nat. Pflanzenf. 3^1: 160, and by Keeble, *loc. cit. supra*.

structure of the host. I would not say that the mistletoe does not gain entrance in these hosts in any other way, but I have seen nothing that would indicate that it does.

In the case of the ash, the mistletoe seeds, *P. villosum*, falling on the younger and smooth branches send out their hypocotyls and these attach themselves at once to the substratum. The branches are provided with prominent lenticels and if one of these chances to be directly beneath a disc, the epidermal cells of the disc enter it, dissolving or pushing to one side, or both, the cells of the host, and at length find themselves in the cortex. This is not a matter of solution entirely, since the host-cells at the side

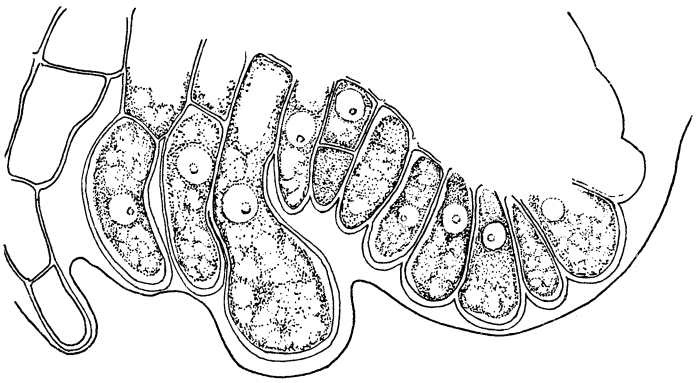

FIGURE 3. Secreting cells at the edge of the disc of such a young mistletoe as that shown in the preceding figure. The cells are evidently active, but a study of the section from which the sketch was made does not show that the host tissues are being dissolved as the sketch would indicate.

of the haustoria give evidence of having been subjected to pressure by them, and the walls of such cells, as will appear directly, are suberized. That is, as far as I have been able to determine, and to express the matter in another way, the cell-walls of the host which make up the lenticels and which had been affected by the solvent, were not suberized, as is shown by the following tests. In the section from which FIGURE 4 was sketched, the walls of the host-cells which were immediately in front of the tip of the haustorium, and for a distance back equal to about one third of its length, gave the cellulose reaction with iodine and sulphuric acid; they were colored blue, while the lignified portions of the central

cylinder, the hard bast, as well as the suberized cork cell-walls were colored yellowish, the reaction for corky and for lignified tissue. And it was observed that the cell-walls of the host adjacent to the upper two thirds of the haustorium reacted to the test for suberized walls, and these were the cells which were seen to be compressed in a direction parallel to the surface of the haustorium, and which probably somewhat earlier had been moistened with the secretions of the haustorium. Naturally the cells nearer the tip of the haustorium, whose walls were of cellulose, gave no indications of pressure. It appears probable, therefore, that the entrance was made by pressing the loosely constructed tissue of the lenticel to one side, and afterwards, when the deeper cortical cells whose walls were of cellulose were reached, the solvents secreted by the haustorium became for the first time of service to the growing root by making the resistance of the host less, as well as by preparing the host-tissues for absorption.

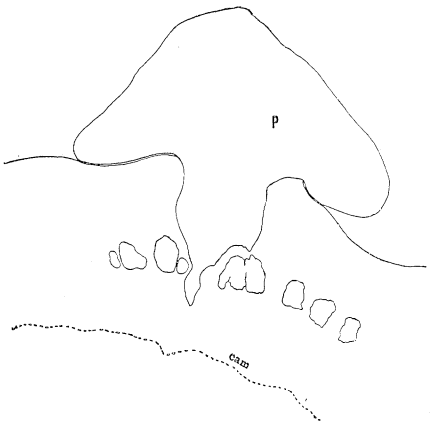

FIGURE 4. *P. villosum* on ash. The haustorium is making its way between the hard bast of the cortex, but does not dissolve them. *p*, mistletoe; *cam*, cambium.

The general forms of haustoria which have penetrated in the manner above outlined, and on this host, as compared with those of the haustoria on the mesquite, point also to this conclusion. In the former the haustoria are most frequently wedge-shaped, in the latter they may be more or less spread out and brush-formed (FIGURE 4) and in the latter also there were no evidences of pressure exerted by the mistletoe on the host's tissues.

Penetration in the other species, it can thus be seen, takes place in quite another manner. This presumably, in part at least, is due to the differences in the structure of the branch of the two hosts. The axillary buds of the mesquite are closely enwrapped by protecting scales, and the internodal portions of the branch are

usually somewhat roughened and appear not to bear lenticels. Therefore the mistletoe seedling that would penetrate the mesquite branch must be able to make its way through the outer cork either by pressure or by dissolving the periderm, or entrance must be gained at some other point, as at the axillary buds. The latter solution of the problem has been made.

Even in older mistletoe plants it frequently happens that one can identify their place of attachment as being axillary, and in the younger ones the host sometimes sends out leaves from the same

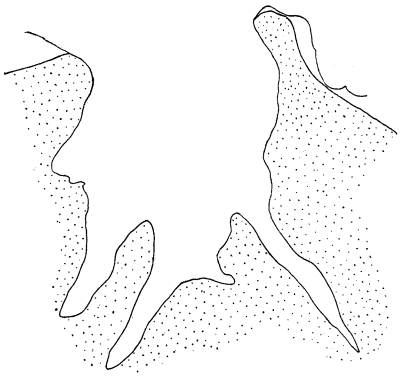

FIGURE 5. *P. Californicum* penetrating the cortex of the mesquite; the branching of the haustorium, which frequently may be seen, is shown.

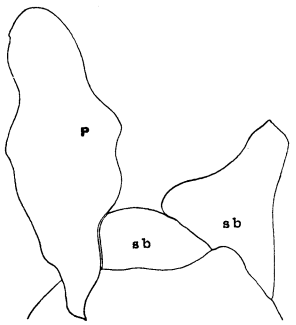

FIGURE 6. *P. Californicum* entering the cortex of the mesquite in the region of the axillary bud. *p*, mistletoe seedling; *sb*, the scale bases.

axillary buds. And I have seen branches of the mesquite on which as many as half-a-dozen successive buds bore mistletoes.

The manner of infection is as follows: seedlings which are attached to the internodal portion of the branch secrete solvents, as the discoloration of the cork immediately under the discs of the haustoria show, but they do not effect the penetration; such seedlings, however, as are attached either to the buds, or to the branch but close to them, and whose hypocotyls reach the buds, are those which at length gain admission into the sub-cortical host-tissues. The hypocotyls are pushed between the bud-scales to their base, the discs are formed in that position, and the secreting cells are thus brought at once in contact with cellulose cell-walls. These are penetrated without difficulty and, as mentioned above, apparently without exerting any pressure on the host (see FIGURE 5).

Although the method of securing an entrance into the hosts is in the two species of mistletoe and the two kinds of host plants above considered unlike in certain particulars, they agree in this, namely, that the solvents secreted by the haustoria of the parasite do not in either case dissolve suberized cell-walls, and apparently cannot do so. For this reason the points of admission open to the mistletoe are determined solely by the character of the host-substratum, whether its cells are loosely put together, as in the lenticels of the cottonwood, or the place where the parasite seeks admission has cellulose cell-walls.

Finally, it should be stated that the above conclusion is based on anatomical evidence alone, and that the subject should be taken up from the experimental standpoint before the conclusion can be definitely accepted as valid. And this experimental work I hope sooner or later to undertake.

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